J. HYM. RES.
Vol. 8(1), 1999, pp. 74–97

Deceptive Similarity in Army Ants of the Genus *Neivamyrmex* (Hymenoptera: Formicidae): Taxonomy, Distribution and Biology of *N. californicus* (Mayr) and *N. nigrescens* (Cresson)

PHILIP S. WARD

Department of Entomology, University of California, Davis, California 95616, USA

Abstract.—The army ant *Neivamyrmex californicus* (Mayr) is demonstrated to be a distinct species, endemic to California and adjacent Baja California, whose range overlaps that of *N. nigrescens* (Cresson), with which it has been previously confused. *N. nigrescens* is widespread throughout the southern Nearctic region, and shows extensive morphological variation in shape, size and sculpture. In the northwestern extremities of its range (i.e., north-central California, Nevada, Utah, and southwestern Colorado) *N. nigrescens* is convergently similar to *N. californicus* in certain aspects of worker morphology: workers lack the densely punctulate head sculpture typical of this species, and in their more shiny appearance they are superficially similar to workers of *N. californicus*. Many records of "*N. californicus*" (and the description of its supposed queen) actually refer to this shiny morph of *N. nigrescens*. That the shiny form is conspecific with, although partially differentiated from, other populations of *N. nigrescens* is indicated by the occurrence of intermediate populations in a relatively narrow transition zone in the San Gabriel Mountains of southern California. No intermediates have been observed between *N. nigrescens* and *N. californicus*. The latter species appears to be more closely related to *N. opacithorax* Emery than to *N. nigrescens*. In California *N. nigrescens* and *N. californicus* raid the nests of other ants, including *Messor andrei*, *Pheidole californica*, *P. hyatti*, *Solenopsis molesta*, and *Formica moki*. Field observations, combined with indirect evidence from the contents of ant nest middens, suggest considerable overlap in prey choice and habitat use. Both *N. nigrescens* and *N. californicus* are commonly sympatric in southern California (where *N. nigrescens* retains its distinctive granular-punctulate body sculpture), but less frequently so in northern California where they are more similar in appearance, and where *N. californicus* tends to be confined to more mesic, coastal areas than *N. nigrescens*.

Army ants in the genus *Neivamyrmex* are a frequent component of ant communities in tropical and warm temperate regions of the New World. The group has received considerable attention from taxonomists (e.g., Smith 1942; Borgmeier 1953, 1955, 1958; Watkins 1976, 1982, 1985), with the resulting recognition of about 120 species (Bolton 1995). Taxonomic problems persist, however, partly because many names are based on either workers or males only—and the names for the two castes are not yet cross-referenced and synonymized—but also because there is substantial and often confusing intraspecific variation in morphology (Smith 1942). Such variation is not unexpected given that the reproductive females (queens) of these and other army ants are entirely wingless and have quite limited powers of dispersal (Gotwald 1995), a factor that favors population differentiation.

The present contribution is concerned with clarifying the taxonomy of *Neivamyrmex californicus* (Mayr) and several closely related species. Earlier treatments of these species are shown to be misleading. Simple morphometric analyses help to resolve and diagnose *N. californicus* and *N. nigrescens* (Cresson), two species whose taxonomic distinctness was previously called into question (Watkins 1985). Both these species—but especially *N. nigrescens*—show considerable variation in integu-

ment sculpture, and this phenomenon misled earlier investigators about species limits.

The range of *Neivamyrmex californicus* is more restricted than previously thought, the species being confined to the Californian floristic province (California and adjacent northern Baja California), where it is broadly sympatric with *N. nigrescens*. The latter is shown to be a highly polytypic species with an extensive transcontinental distribution.

MATERIALS AND METHODS

Specimens were examined in the following collections:

CASC California Academy of Sciences, San Francisco, California, U. S. A.
CDAE California Department of Food & Agriculture, Sacramento, California, U. S. A.
JTLC John T. Longino Collection, Olympia, Washington, U. S. A.
LACM Natural History Museum of Los Angeles County, Los Angeles, California, U. S. A.
MCZC Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U. S. A.
MHNG Muséum d'Histoire Naturelle, Geneva, Switzerland
NHMV Naturhistorisches Museum, Vienna, Austria
RAJC Robert A. Johnson Collection, Tempe, Arizona, U. S. A.
UCDC Bohart Museum of Entomology, University of California, Davis, California, U. S. A.
USNM National Museum of Natural History, Smithsonian Institution, Washington, D. C., U. S. A.

Other collections cited are:

ANSP Academy of Natural Sciences, Philadelphia, U. S. A.
MCSN Museo Civico di Storia Naturale, Genoa, Italy

The following measurements and indices were used for workers and queens. All measurements were taken at 50× magnification with a Wild M5A microscope and a pair of Nikon stage micrometers wired to a digital readout. Measurements were recorded to the nearest thousandth of a millimeter.

HW Maximum width of head, measured in full-face (frontal) view
HL Maximum length of head in frontal view, from the midpoint of a line drawn across the posterior margin to the anteriormost point on the clypeal margin. This *excludes* the thin, lamelliform clypeal apron, which projects forward from the clypeal margin and may be partly hidden by the mandibles.
MFC Minimum distance between the frontal carinae
SL Length of the scape, excluding the basal neck
WL Weber's length: length of the mesosoma, as seen in lateral view, from the anterior pronotal margin (excluding the collar) to the posterior extremity of the metapleuron
PL Length of the petiole, measured in lateral view along the long axis of the petiole, from the anterior margin (excluding the short peduncle) to the posterior extremity
PH Petiole height, measured at right angles to PL, from the summit of the petiole to the petiolar venter, excluding the anteroventral tooth (if present)
DPW Maximum dorsal width of the petiole, measured in dorsal view
PPW Maximum dorsal width of the postpetiole, measured in dorsal view
MTL Length of the metatibia, excluding the basal condyle (Fig. 3)
QGL Length of the gaster (queen caste only), measured in lateral view from the posterior end of the gas-

ter to the anterior extremity of abdominal segment 3, excluding the helcium. This measurement was taken only on non-physogastric queens.

CI Cephalic index: HW/HL
SI Scape index: SL/HW
FCI Frontal carinal index: MFC/HW
PLI Petiole length index: PH/PL
PWI Petiole width index: DPW/PL
MTI Metatibial index: MTL/HW

Neivamyrmex californicus and allied species.

Among the North American army ants of the genus *Neivamyrmex* three species—*N. californicus*, *N. nigrescens* and *N. texanus*—can be diagnosed in the worker caste by having a mandible whose basal margin rounds gradually into masticatory margin, without an angular junction (Figs. 1, 4, 7). The species have many other traits in common, including: moderately large size (HW 0.60–1.42); well developed clypeal apron; relatively prominent ocellus-like eye with convex surface; weakly developed occipital lobes; lamellate and ventrally directed lower pronotal flange; petiole longer than high (PLI 0.68–0.96) and markedly longer than wide (PWI 0.52–0.74); and dense punctulate sculpture covering part of the body but without conspicuous overlying coarse impressions or rugae.

These taxa are part of a larger group of species, including *N. chamelensis* Watkins, *N. cornutus* Watkins, *N. manni* (Wheeler), *N. opacithorax* (Emery) and *N. sumichrasti* (Norton), that can be placed together, on the basis of similarities in worker morphology and male genitalia, in an assemblage of *Neivamyrmex* species termed "Gruppe VI" by Borgmeier (1955: 490). Although the three species treated in this paper are evidently closely related, their exact phylogenetic relationship to one another and to these other taxa remains to be resolved.

List of species considered here, with known castes (w = worker, m = male, q = queen) and distribution:

californicus (Mayr 1870) (w)
U. S. A.: California
Mexico: Baja California

nigrescens (Cresson 1872) (w, q, m)
U. S. A.: California, Nevada, Utah, Arizona, New Mexico, Colorado, and east-central United States
Mexico: Baja California, Baja California Sur, Jalisco, Nayarit, Oaxaca, San Luis Potosí, Sonora, Tamaulipas

texanus Watkins 1972 (w, q, m)
U. S. A.: Arizona, New Mexico, Colorado, and east-central United States
Mexico: Chihuahua, Durango, Hidalgo, Jalisco, Nuevo León, San Luis Potosí, Sonora

SPECIES ACCOUNTS

Neivamyrmex californicus (Mayr 1870) (Figs. 1–3, 10)

Eciton californicum Mayr 1870: 969. Nineteen syntype workers, San Francisco (Schaufuss) (NHMV) [examined]. One syntype worker here designated **lectotype**.

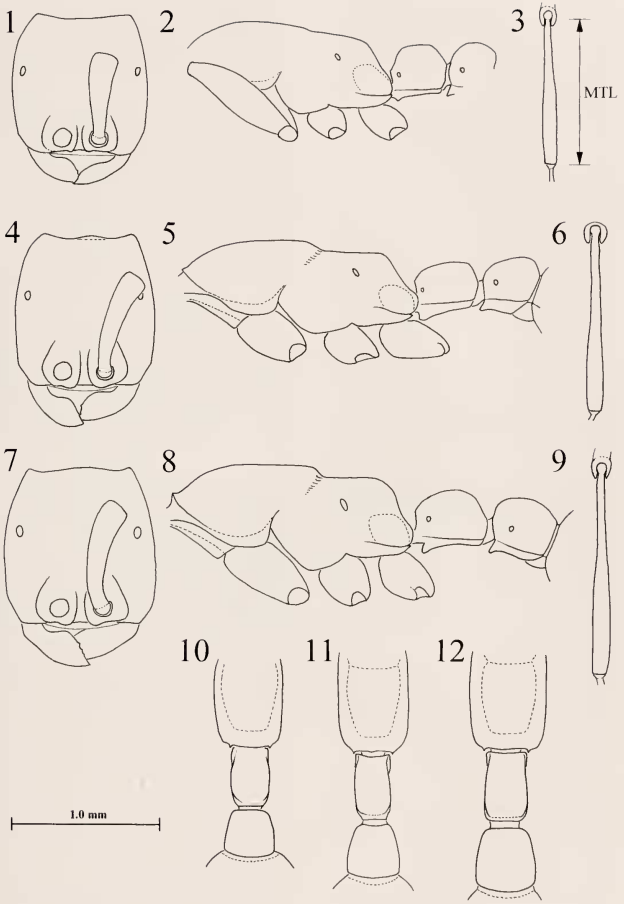
Eciton (*Acamatus*) *californicum* Mayr; Emery 1894: 182.

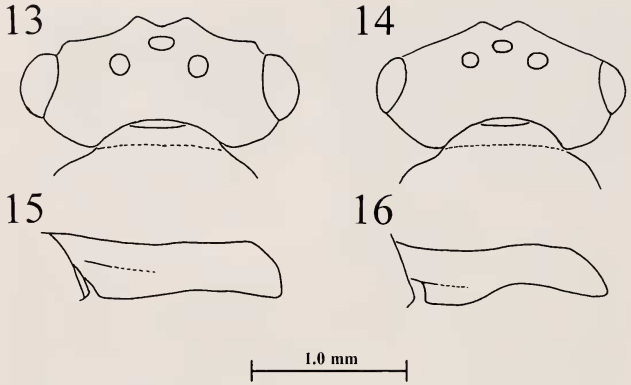
Eciton (*Acamatus*) *californicum* var. *obscura* Forel 1914: 265. Two syntype workers, Vista, California (E. Hindle) (MHNG) [examined]. One syntype worker here designated **lectotype**. Synonymy by Borgmeier 1955: 517; here confirmed.

Eciton (*Neivamyrmex*) *californicum* Mayr; Smith

→

Figs. 1–12. *Neivamyrmex* workers, full-face view of head (1, 4, 7), lateral view of mesosoma, petiole and postpetiole (2, 5, 8), lateral view of metatibia (3, 6, 9), and dorsal view of propodeum, petiole and postpetiole (10–12). 1–3, 10: *N. californicus*, San Francisco, California, lectotype worker; 4–6, 11: *N. nigrescens*, shiny form, 2km SE Mt. Vaca, California; 7–9, 12: *N. nigrescens*, typical form with opaque head, Sevilleta NWR, New Mexico. Fig. 3 indicates measurement of MTL.


1
2
3
MTL
4
5
6
7
8
9
10
11
12
1.0 mm



Figs. 13–16. *Neivamyrmex* males, dorsal view of head (13, 14) and lateral view of left paramere (15, 16). 13, 15: *N. nigrescens*, Ash Mountain Kaweah Power Stn.#3, Tulare Co., California; 14, 16: *Neivamyrmex* species, probably *opacithorax*, same locality.

1942: 560. First combination in subgenus *Neivamyrmex*, but the material examined and described by M. R. Smith was *N. opacithorax* not *N. californicus*.

Neivamyrmex californicus v. *obscurus* (Forel); Borgmeier 1953: 8.

Neivamyrmex californicus (Mayr); Borgmeier 1953: 11.

Neivamyrmex californicus (Mayr); Borgmeier 1955: 517.

Neivamyrmex californicus (Mayr); Watkins 1972: 363 (part). Description of queen (p. 364) is that of *N. nigrescens*, not *N. californicus*.

Neivamyrmex californicus (Mayr); Watkins 1985: 482 (part). Key (p. 482) and distribution map (figure 4, p. 500) refer partly to *N. californicus* and partly to *N. nigrescens*.

Worker measurements.—(n = 28). HW 0.63–1.10, HL 0.69–1.11, WL 1.03–1.67, MTL 0.68–1.18, CI 0.86–1.00, FCI 0.033–0.061, SI 0.68–0.80, MTI 1.05–1.14, PLI 0.78–0.88, PWI 0.62–0.73.

Worker description.—Body of moderate size (see HW, HL and MTL measurements) and somewhat compact (see plot of WL on HW; Figs. 19, 23); head broad, CI approaching 1.00 in largest workers, i.e., those in which HW and MTL > 1.00 mm; mandible with basal margin rounding gradually into masticatory margin (Fig. 1); masticatory margin with a small tooth at the terminus of this rounding, followed by 1–4 denticles (tending to increase in size), then a more prominent tooth midway along the margin; distal portion of masticatory margin generally edentate (a small denticle or two may follow the mid-point tooth) except for the acute apical tooth; anterior margin of torulus separated from anterior margin of clypeus (ignoring the thin diaphanous clypeal apron) by about 0.2× the diameter of the torulus; frontal carinae moderately well separated (MFC 0.022–0.061), diverging anteriorly, and protruding very slightly (largest workers) or not at all (most workers) beyond the anterior clypeal margin, when the head is seen in frontal view; anterior clypeal margin more or less straight (weakly convex

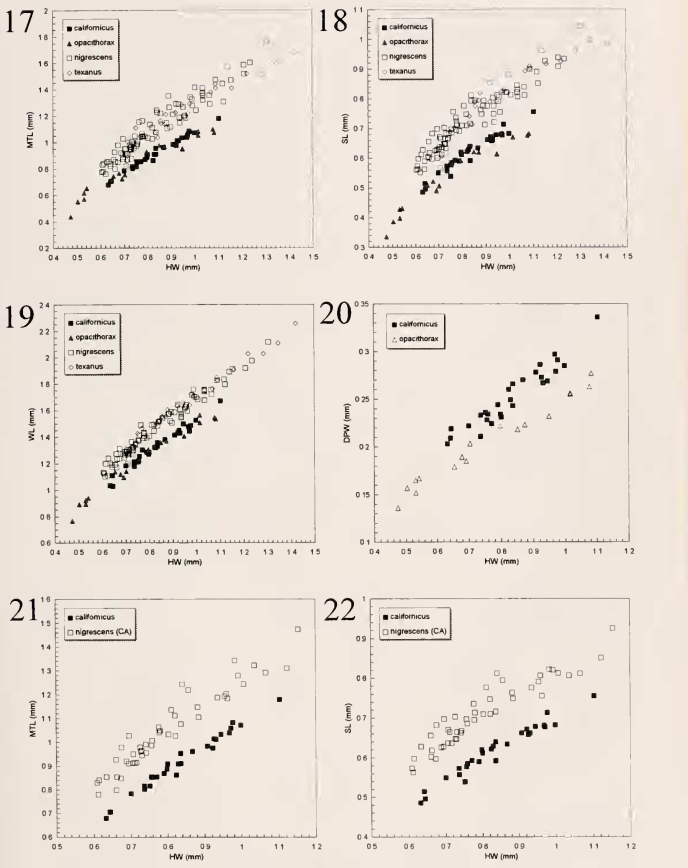
in smallest workers, and slightly concave in largest workers); clypeal apron relatively well developed, its anterior margin generally slightly convex or subangulate; clypeal apron extending anteromedially beyond the clypeal margin proper by a distance equal to 0.4–0.5× the torulus diameter; each compound eye consisting of a single convex ommatidium, breaking the surface of the head, its maximum diameter approximately 0.06–0.08 mm (6–10% of head width); scapes of moderate length, exceeding the eye when held back against the head (SI 0.68–0.80; SI2 0.67–0.75) (see also plot of SL on HW and SI on MTL; Figs. 18, 22, 26); posterior margin of head usually concave, in frontal view; occipital lobes weakly developed, not protruding conspicuously when the head is seen in frontal view; anterior pronotum descending gradually towards the collar, transverse ridge weakly developed; lower pronotal flange thin, lamellate, directed more or less ventrally; dorsal profile of mesosoma rather flat, and dorsal face of propodeum only slightly depressed below the level of the mesonotum (Fig. 2); dorsal face of propodeum rounding into, and subequal in length to, the declivitous face; latter flat to weakly concave, in profile; legs relatively short, MTL/HW (=MTI) < 1.15; petiole short, high, and with short vertical anterior face, followed by a more or less evenly convex dorsal surface (as seen in profile; Fig. 2), or with a slightly steeper posterodorsal than anterodorsal slope; in dorsal view, petiole subrectangular, but with somewhat convex sides, about 1.5 times longer than wide; anteroventral process of petiole a thickened transverse shelf, in lateral view appearing as a relatively small, blunt tooth directed anteroventrally; a similar, less protrusive structure at the anteroventral extremity of the postpetiole; in dorsal view postpetiole subtrapezoidal (Fig. 10), with straight, diverging sides, broadest posteriorly, and slightly broader than long. Upper surface of mandible finely and densely striate with scattered punctures, subopaque, lateral surface of mandible and area immediately preceding the masticatory margin smooth and shiny with scattered punctures. Head largely smooth and shining, with numerous piligerous punctures separated by several to many diameters; in larger workers (and in more southern populations) the punctures may be coarser and denser, and parts of the intervening shiny integument dulled very slightly by weak reticulation. Mesosoma densely punctulate, opaque, but in smaller workers the sculpture weakened laterally on the pronotum (which becomes finely reticulate and sublucid) and replaced by smooth shiny areas on the dorsum of the promesonotum. In workers of all sizes, including heavily sculptured large individuals, the center of the mesonotum is nearly always smooth and shiny, with a few larger piligerous punctures, and contrasts with the predominantly punctulate and opaque dorsal face of the propodeum (exceptions include some heavily sculptured workers from southern California in which the mesonotum center is weakly reticulate and sublucid, but still contrasts with the opaque dorsal surface of the propodeum; and small, shiny workers from northern California in which even the propodeum dorsum loses its punctulate sculpture centrally, so that contrast between the mesonotum and the propodeum is lessened). Petiole laterally reticulo-punctate and subopaque to sublucid, petiolar dorsum mostly shining, but with variable traces of punctulate reticulation; postpetiole and gaster smooth and shiny, with scattered piligerous punctures. Long, fine, golden pilosity conspicuous on body and appendages (scape, funiculus, legs), mostly suberect to subdecumbent. Body light castaneous brown to deep reddish-brown, tending towards a lighter yellow-brown on the postpetiole and gaster. Mandible medium to dark brown, usually contrasting somewhat with the lighter head color.

Queen.—Unknown. The "*N. californicus*" queen from Davis, California, described by Watkins (1972), is that of the shiny form of *N. nigrescens*. A single queen, in rather poor condition, from Monterey, California (31.v.1963; leg. Roy Johnson; USNM), could be either *N. opacithorax* or *N. californicus*. It is relatively small in size (HW 1.65, WL 2.68, MTL 1.33), with short scapes (SI 0.46), rounded occipital lobes, short legs (MTI 0.81), and a long gaster (QGL/WL = 2.34). The short appendages and elongate gaster are features that distinguish *N. opacithorax* queens from those of *N. nigrescens*, but they might also be characteristic of *N. californicus*. There are apparently no worker specimens associated with the Monterey queen, leaving its specific identity uncertain.

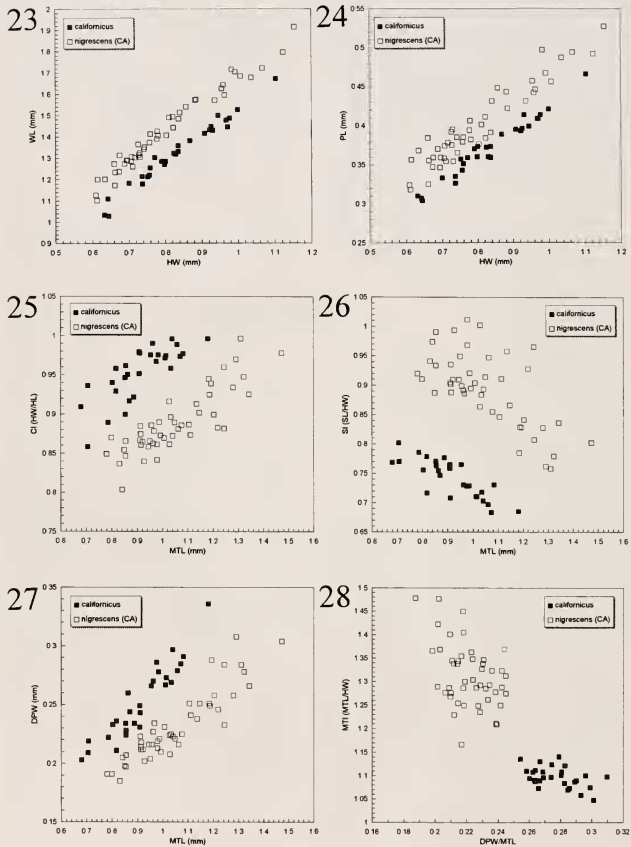
Male.—Unknown. In LACM and CASC there are a series of *Neivamyrmex* males, collected in California but unassociated with workers, that appear to be *N. opacithorax* on the basis of head shape and (especially) male genitalia (Figs. 14, 16). The proximal flange on the ventral margin of the paramere would seem to be particularly characteristic of that species. Nevertheless, until worker-associated males of *N. californicus* are discovered, one cannot exclude the possibility that some of these males (from Contra Costa and Tulare Counties) represent *N. californicus*.

Comments.—Workers of *N. californicus* can be distinguished from those of *N. nigrescens* by their more compact body, shorter legs and scapes, and broader head and petiole (Figs. 1–3). The simplest quantitative diagnostic is the metatibial index (MTI = MTL/HW) which ranges from 1.05 to 1.14 in *N. californicus* (n = 28) compared to 1.16 to 1.52 in *N. nigrescens* (n = 89). A bivariate plot of the relevant measurements (MTL and HW) demonstrates the distinction (Fig. 17). Other differences between *N. californicus* and *N. nigrescens* are captured by plots of scape length (SL) on head width (HW) and Weber's length (WL) on head width (Figs. 18, 19, 21, 22). When samples from all populations of *N. nigrescens* are considered (i.e., including workers from the Southwest and from eastern United States) there is a slight overlap in the distribution of points (Figs. 18, 19); but when confining the comparisons to populations of *N. nigrescens* that are sympatric with *N. californicus* (i.e., populations from California) these and other bivariate plots produce non-overlapping clouds of points (see Figs. 21–28). Because of allometry, neither the cephalic index (CI = HW/HL) nor the scape index (SI = SL/HW) are diagnostic in themselves, but when plotted against the metatibia length (MTL) a sharp distinction is seen between the two species (Figs. 25–26). Thus, within a given size class (as measured by MTL) there is no overlap in CI or SI; but small workers of *N. californicus* have scape and cephalic indices that overlap with large workers of *N. nigrescens*.

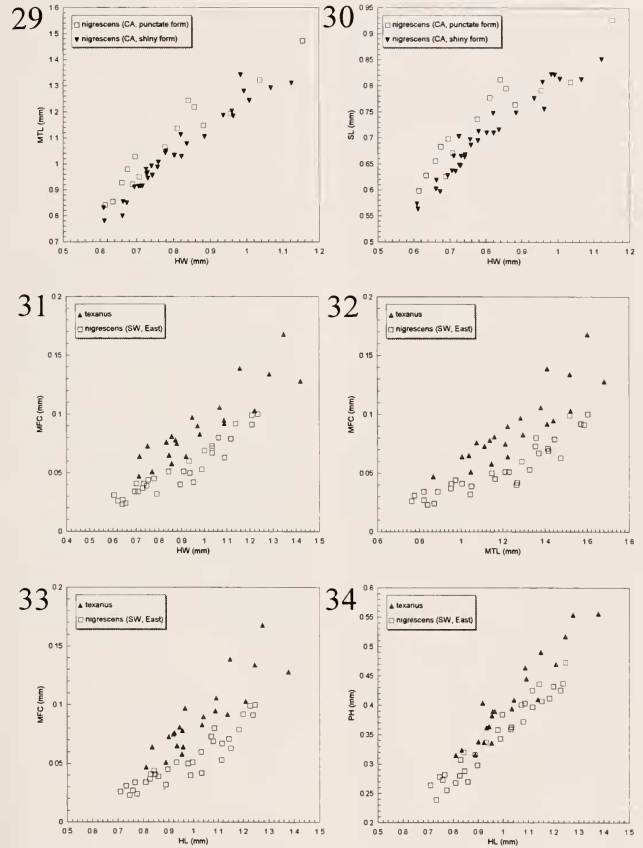
Workers of *N. californicus* also have the dorsal face of the propodeum less depressed below the level of the mesonotum than in *N. nigrescens* (compare Figs. 2 and 5), and this difference is diagnostic. Less tangible are differences in body sculpture: the dense punctulate sculpture that is so prominent in most populations of *N. nigrescens* and that imparts a granular appearance to the head and mesosoma is much less developed in *N. californicus*, such that the head, mesonotum, and postpetiole are largely smooth and shiny (covered only with scattered piligerous punctures). But a reliance on sculptural differences led to the past confusion between these two species: populations of *N. nigrescens* that are broadly sympatric with *N. californicus* in central and northern California also have weakened body sculpture and are superficially similar to those of *N. californicus*. On average, *N. californicus* is still the shinier of the two (see distinctions in key couplet 9A below) but the differences are subtle. The contrasts in body shape and leg length documented



Figs. 17–22. Bivariate plots of various metric measurements in workers of four species of *Neivamyrmex*.



Figs. 23–28. Bivariate plots of metric measurements and indices in workers of *Neivamyrmex californicus* and *N. nigrescens* (California populations only).



Figs. 29–34. Bivariate plots of metric measurements and indices in workers of *Neivamyrmex texanus* and various populations of *N. nigrescens*.

above are more reliable for distinguishing these two species.

N. californicus differs more obviously from *N. texanus*. Like *N. nigrescens*, workers of *N. texanus* have longer legs (MTI 1.18–1.48), longer scapes (SI2 0.75–0.89), and a more gracile body than those of *N. californicus*. They also average larger in size, have more widely separated frontal carinae (FCI 0.066–0.125 compared to 0.033–0.061 in *N. californicus*), and have a consistently opaque, densely punctulate head and mesosoma such that they are unlikely to be confused with *N. californicus* workers. As far as known, the ranges of the two species do not overlap (Fig. 36).

The bivariate plots of measurements (Figs. 17–19) show that in many respects *N. californicus* is more similar to *N. opacithorax* than to *N. nigrescens* or *N. texanus*. *N. opacithorax* can be distinguished from *N. californicus* by the angular basal margin of the mandible; shorter clypeal apron; narrower petiole (Fig. 20); and different pattern of body sculpture (side of pronotum usually smooth and shiny, and contrasting with the rugulose-punctulate mesosoma dorsum).

Material examined.—(CASC, CDAE, JTLC, LACM, MCZC, MHNG, NHMV, RAJC, UCDC, USNM)

MEXICO **Baja California**: 28km E Ensenada, 750m (P. S. Ward).

UNITED STATES **California** *Contra Costa Co.*: 9km ENE Danville, 490m (P. S. Ward); *El Dorado Co.*: 14km NW Shingle Springs, 340m (P. S. Ward; G. C. Snelling); *Los Angeles Co.*: Arcadia (c.u.); La Verne (A. C. Oberle); Los Angeles (A. Mallis & J. Schwartz); *Monterey Co.*: Salinas (B. Oliver & J. Bunch); *Orange Co.*: Irvine Park (A. Mintzer); Laguna Hills (R. J. Hamton); Limestone Canyon, El Toro Rd., 1.8mi E Cooks Corner (A. Suarez); Tonner Canyon (W. P. Mackay); *Riverside Co.*: Riverside (K. Cooper; K. W. Cooper; E. I. Schlinger); Temecula (A. Suarez); *San Bernardino Co.*: Chino Hills State Park (G. C. Snelling *et al.*); Chino Hills State Park, 700 ft. (R. A. Johnson); *San Diego Co.*: 5mi. NE Poway, 600m (M. S. Trepanier); Camp Pendleton (J. H. Hunt); Chula Vista, E end, 160m (P. S. Ward); Chula Vista, 70m (A. Suarez); Elliott Reserve, 150m (A. Suarez); La Jolla (c.u.); Mt. Laguna, MSP site, 6050 ft. (J. H. Hunt); National City (K. Ross); San Diego (c.u.); Vista (E. Hindle); *San Francisco Co.*: San Francisco (Schaufuss); *San Mateo Co.*: Jasper Ridge, 150m (K. G. Human; N. J. Sanders); *Santa Barbara Co.*: 9km N Goleta, 490m (P. S. Ward); Cachuma Saddle, 1100m (J. Longino); *Santa Clara Co.*: 11km S Palo Alto, 490m (P. S. Ward); *Santa Cruz Co.*: Santa Cruz (K. Brown).

Neivamyrmex nigrescens (Cresson 1972)
(Figs. 4–9, 11–12)

Labidus nigrescens Cresson 1872: 194. Holotype male, Bosque Co., Texas (Belfrage) (ANSP) [not examined].

Eciton nigrescens (Cresson); Dalla Torre 1893: 5.

Eciton (*Acamatus*) *schmitti* Emery 1894: 183. Syntype workers, Doniphan, Missouri (Pergande) (MSCN) [not examined], MCZC, USNM [examined]. Synonymy by M. R. Smith 1938: 160.

Eciton (*Labidus*) *nigrescens* (Cresson); Emery 1895: 258.

Eciton (*Acamatus*) *nigrescens* (Cresson); Emery 1900: 187.

Eciton sumichrasti; Wheeler (nec Norton) 1900: 564. Description of queen (as "*E. sumichrasti*").

Eciton (*Neivamyrmex*) *nigrescens* (Cresson); Smith 1942: 550 (part). Description of worker (part), queen and male.

Eciton (*Neivamyrmex*) *californicum*; Creighton (nec Mayr) 1950: 70 (part).

Neivamyrmex nigrescens (Cresson); Borgmeier 1953: 6.

Neivamyrmex nigrescens (Cresson); Borgmeier 1955: 494 (part). Description of worker (part) and queen. Male (p. 496) is that of *N. texanus* (Watkins 1972).

Neivamyrmex sp. c; Borgmeier 1955: 531. Description of male.

Neivamyrmex nigrescens (Cresson); Watkins 1972: 358.

Neivamyrmex californicus; Watkins (nec Mayr) 1972: 363 (part). Description of queen (as "*N. californicus*").

Neivamyrmex nigrescens (Cresson); Watkins 1985: 482.

Neivamyrmex californicus; Watkins (nec Mayr) 1985: 482 (part).

Worker measurements.—(n = 89). HW 0.60–1.31, HL 0.71–1.31, WL 1.10–2.12, MTL 0.76–1.76, CI 0.80–1.00, FCI 0.030–0.106, SI 0.75–1.01, MTI 1.16–1.52, PLI 0.68–0.91, PWI 0.52–0.71.

Worker diagnosis.—Moderately large body size (see HW, HL and MTL measurements); mandible with basal margin rounding gradually into masticatory margin (Figs. 4, 7); frontal carinae moderately well separated (MFC 0.021–0.138); clypeal apron well developed and, in all but the largest workers, produced anteromedially by an amount subequal to, or greater than, the minimum distance between the frontal carinae (MFC); scapes relatively long, SI > 0.69 (see also plot of SL on HW and SI on MTL; Figs. 18, 22, 26); occipital lobes weakly to moderately developed; anterior margin of pronotum with transverse ridge generally well developed; dorsal (= basal) face of propodeum conspicuously depressed below the level of the promesonotum (Figs. 5, 8), and rounding into the declivitous face, the latter more or less flat (or weakly concave) in profile; legs relatively long, MTL/HW (=MTI) > 1.15; petiole subrectangular, somewhat variable in shape (see PLI and PWI values), but always longer than high or wide (Figs. 5, 8, 11, 12). Head and mesosoma typically densely punctulate, and having an opaque, granular appearance; populations from northwestern portions of the species' range, however, have the sculpture much weakened such that the head is partly smooth and shining, with scattered piligerous punctures and variable amounts of finer reticulate sculpture that partly dulls the sheen; and in this "shiny morph" the mesosoma is partly sublucid, although with at least weak reticulate-punctulate sculpture on most surfaces. In all populations sculpture weakened on the surface of metapleural gland bulla, such that the lower half or more is smooth (or weakly reticulate) and conspicuously shiny. Petiole densely punctulate, subopaque, postpetiole tending to be more lightly sculptured. Body varying from light castaneous brown to dark reddish-brown, the postpetiole and gaster usually lighter than the rest of body.

Queen diagnosis.—Eye distinct, consisting of single convex ommatidium. Head as broad as, or slightly broader than, long (CI 0.96–1.02, n = 6). Occipital corners generally angular and projecting, but may be weakly angulate or rounded. Pronotum without posterior dorsolateral projection. Propodeum (and sometimes also mesonotum) with a median longitudinal impression. Metatibial index (MTI) 0.89–1.07 (n = 6). Petiole subquadrate, slightly broader than long (PWI approximately 1.1–1.2), with a vertical anterior face that rounds into a flat dorsal face, as seen in lateral view. Petiole width much less than the length of the metatibia, DPW/MTL 0.58–0.72 (n = 6). Length of gaster (nonphysogastric) less than twice WL (QGL/WL = 1.70–1.90, n = 5).

Male diagnosis.—Mandibles broad, spatulate (not sickle-shaped). Ocelli moderate in size and separated from the upper margin of the compound eye by a distance greater than twice the diameter of the median ocellus. Prominent transverse swelling above antennal fossa, discerned most clearly in dorsal view (Fig. 13). Setae on venter of petiole typically short, whitish, and slanted posteroventrally, but in some western populations the setae are longer, golden, and suberect. Gaster typically black or blackish-brown, often reddish-brown in western populations. In profile, paramere (= stipes) linear subrectangular, with an oblique (anterodorsal to posteroventral) posterior margin, and a straight ventral margin, not produced anteroventrally (Fig. 15); posterodorsal extremity with a low, triangular projection (Watkins, 1985, Plate 9, fig. 4), tending to become obsolete in western populations (Fig. 15); volsella unforked, with long, slender upturned apex; aedeagus (=sagitta) with an apically upturned posteroventral process, just exceeding the posterodorsal process (in posterior reach).

Comments.—The characteristics that distinguish workers of *N. nigrescens* from those of *N. californicus* and *N. texanus* are discussed under those respective species.

N. nigrescens differs from *N. opacithorax* by the shape of the worker mandibles, by the heavier body sculpture, especially on the side of the pronotum, by the longer scapes, mesosoma and legs (Figs. 17–19), and by the more strongly convex profile of the promesonotum.

A remaining question concerns the status of the *nigrescens*-like populations with shiny worker heads, that are superficially similar to those of *N. californicus*. This "shiny morph" of *N. nigrescens* is found in north-central California, parts of the Great Basin, and in upper sections of the Colorado River drainage, while the more "typical" form, with densely punctulate and opaque worker head, is distributed widely from southern California, Arizona and adjacent regions of Mexico to southeastern United States (Fig. 37). What happens in zones of contact between the two forms? Records are too sparse to answer this question for the Colorado River basin, but collections from southern California reveal a zone of intergradation centered on the north side of the San Gabriel Mountains. In fact patterns of sculpturation are intermediate in samples taken from this region, so that the distinction between the two "forms" becomes quite arbitrary. For this reason it seems clear that they must be treated as conspecific, although the patterns of distribution are suggestive of a previous period of isolation followed by secondary contact and introgression.

Material examined.—(1) Typical form with opaque, densely punctulate head (CASC, CDAE, LACM, MCZC, RAJC, UCDC, USNM)

MEXICO **Baja California**: 28km E Ensenada, 750m (P. S. Ward); 31.7mi WNW Bahia de los Angeles (Hardy, Andrews & Giuliani); 6mi SE Laguna Chapala (A. E. Lewis); **Baja California Sur**: 12mi S Santa Rosalia (Michelbacher & Ross); 15mi S San Domingo (Ross & Bohart); 20mi W La Paz (E. L. Sleeper); 26km NW Santa Rosalia (R. A. Johnson); Coyote Cove, Conception Bay (Michelbacher & Ross); Isla San José, 1mi S Punta Colorada [as "Punta Colorado"] (J. T. Doyen); San Hilario (E. L. Sleeper); San Ignacio, 140m (M. Bennett); **Jalisco**: 3mi SE Plan de Barrancas (F. D. Parker & L. A. Stange); **Nayarit**: *Islas Tres Marias*: Isla Cleofas (R. R. Snelling); Isla Magdalena (R. R. Snelling); **San Luis Potosí**: Cd. Valles, El Bañito (J. F. Watkins); **Sonora**: 2km N Bahía de la Cruz, Isla Tiburón, 10m (P. S. Ward); 2km SW Punta Narragansett, Isla Tiburón, 5m (P. S. Ward); 37mi N Hermosillo, 1700 ft. (R. R. Snelling); 5mi S Cananea (V. D. Roth); 8km N Desemboque de los Seris (R. A. Johnson); Los Horcones, Rte. 16, 4km E La Colorada (B. Bestelmayer); **Tamaulipas**: Cd. Victoria (J. F. Watkins).

UNITED STATES **Alabama**: *Dallas Co.*: Selma (W. H. Patton); *Jefferson Co.*: Birmingham (R. D. Jordan); *Lauderdale Co.*: Florence (W. Cloyd; F. Moore); *Lawrence Co.*: King Cove, Bankhead Natl. Forest (E. O. Wilson); *Mobile Co.*: Kushla (A. C. Sturtevant); Spring Hill [as "Springhill"] (W. S. Creighton); *Morgan Co.*: Decatur (Murphree); **Arizona**: *Cochise Co.*: 2mi NE Portal (G. D. Alpert); Chiricahua Mts. (W. & E. MacKay; J. F. Watkins); Chiricahua Mts., 5000 ft. (J. F. Watkins); Chiricahua Mtns., 13mi NW jct. Rte. 80 on FSR 74, 5850 ft. (S. P. Cover); Chiricahua Mtns., Cave Creek Canyon, SW Res. Stn., 5400 ft. (S. P. Cover); Copper Canyon, 8.1mi SE Sunnyside, 5900–6000 ft. (R. R. Snelling); Copper Canyon, Huachuca Mtns., 22km SSW Sierra Vista, 1770m (S. G. Brady); Douglas (W. W. Jones); Huachuca Mts., Miller Canyon (A. E. Lewis); Miller Canyon, Huachuca Mtns., 6000 ft. (W. M. Wheeler); Palmerlee, Huachuca Mtns., 5300 ft. (W. M. Wheeler); Paradise Rd., 1.3mi W Portal Rd. Chiricahua Mts. (G. C. Snelling); Portal (Gotwald); Ramsey Canyon, Huachuca Mts. (W. S. Creighton); Ramsey Canyon, Huachuca Mts., 5800 ft. (W. M. Mann); SWRS, Portal, 5600 ft. (W. S. Creighton); Texas Pass, Dragoon [as "Dragon"] Mtns. (W. M. Wheeler); *Gila Co.*: Pinal Mts., 8000 ft. (R. A. Flock); Sierra Anchas, Hwy. 288 at Exp. Res. Stn., 4800 ft. (R. A. Johnson); *Maricopa Co.*: Four Peaks Wilderness, nr. Pidgeon Springs, 5600 ft. (R. A. Johnson); Mazatzal Mtns., on Four Peaks Rd., 10.3mi E Hwy. 87, 4000 ft. (R. A. Johnson); South Phoenix Park (P. S. Ward); *Mojave Co.*: Hualapai Mts., s. of Kingman, 1450m (E. I. Schlinger); *Pima Co.*: Baboquivari Mtns, Forestry Cabin, 3500 ft. (W. S. Creighton); Buehman Canyon, Santa Catalina Mts., 2900–3000 ft. (R. R. Snelling & G. C. Snelling); Santa Catalina Mts. (M. Chrisman); Tucson (R. H. Crandall); *Pinal Co.*: Oracle, 4500 ft. (W. M. Wheeler); *Santa Cruz Co.*: 6.7mi W I-19 on Ruby Rd. (G. C. Snelling); Bog Springs Cpgrd., Madera Canyon, Santa Rita Mts. (G. C. Snelling); Madera Canyon (R. H. Crandall); Madera Canyon, Santa Rita Mts. (R. H. Crandall); Nogales (Ehringer); Pajarito Mtns., Ruby Rd., 6.7mi W I-10, 4000 ft. (R. A. Johnson); Peña Blanca Lake (B. V. Brown & D. H. Feener); Ruby Rd., 7mi W Peña Blanca (G. C. Snelling); *Yavapai Co.*: 7.2mi E Chino Valley, 4600 ft. (R. A. Johnson); *Yuma Co.*: Burro Cyn., 2mi SE jct. 24, Kofa Game Refuge (P. Melhop & R. R. Snelling); **California**: *Los Angeles Co.*: Claremont (B. Crow); E fork, San Gabriel R., Angeles N. F.

(C. Ishida); Eaton Canyon (Sutton?); Eaton Canyon Pk. (R. H. Crandall); Jct. Angeles Crest & Angeles Forest Hwys. (G. C. Snelling); Millard Canyon, San Gabriel Mts. (R. H. Crandall); Placerita Canyon Park (F. T. Hovore); *Orange Co.*: Tonner Canyon (W. P. MacKay); *Riverside Co.*: Camino Rosales (A. Suarez); Margarita Summit (A. Suarez); near Perris (Mallis, Zschokke & Schwartz); Pinyon Flat, 1220m (P. S. Ward); Riverside (K. W. Cooper; M. E. Irwin); San Timoteo Cyn. (M. Wasbauer & A. Hardy); Temecula Cyn., Sta. Margarita R. (E. I. Schlinger); *San Bernardino Co.*: 2mi E Mentone (W. S. Creighton); Aliso Cr., Chino Hills State Park (M. Bennett *et al.*); Chino Hills State Park, 700 ft. (R. A. Johnson); *San Diego Co.*: 18km E Mt. Laguna, 300m (P. S. Ward); 5mi N Descanso, MSP primary site, 3000 ft. (J. H. Hunt); 5mi. E La Jolla (M. S. Trepanier); Chula Vista (E end), 160m (P. S. Ward); La Jolla (M. S. Trepanier); La Mesa (F. X. Williams); Nate Harrison Rd. nr. Mt. Palomar, 4800 ft. (E. I. Schlinger); nr. La Mesa (F. X. Williams); Point Loma (P. Leonard; A. Suarez); Ramona, 450m (M. S. Trepanier); San Diego (c.u.); **Colorado**: *Chaffee Co.*: Salida (c.u.); Salida, 7050 ft. (W. M. Wheeler); **Georgia**: *Jackson Co.*: Commerce (Vanderford); **Illinois**: *Adams Co.*: Quincy (T. E. Musselman); *Johnson Co.*: Ferne Clyffe St. Pk. (W. S. Creighton); **Iowa**: *Harrison Co.*: Little Sioux (W. F. Buren); *Woodbury Co.*: Sioux City (C. N. Ainslie; W. F. Buren); **Kansas**: *Douglas Co.*: Lawrence (F. X. Williams); Nat. Hist. Reser., Lawrence (C. W. Rettenmeyer); *Harvey Co.*: Sedgwick [as "Sedwick"] (A. J. McCurray); *Jefferson Co.*: Valley Falls (A. Mattis); *McPherson Co.*: McPherson (W. Knaus); *Pottawatomie Co.*: Onaga (F. F. Crevecoeur); *Riley Co.*: Jardine Terr. (J. F. Watkins); Manhattan (A. J. Mattis; R. C. Smith); no specific locality (F. Marlatt; J. B. Norton; J. F. Watkins); *Sedgwick Co.*: Wichita (J. R. Horton); **Kentucky**: *Marshall Co.*: Kentucky Dam (W. L. Brown); **Louisiana**: *Acadia Co.*: Crowley (C. E. Hood); *Beauregard Co.*: DeRidder (W. F. Buren); *East Baton Rouge Co.*: Baton Rouge (T. H. Jones); *Lafayette Co.*: Lafayette (E. S. Tucker); *Madison Co.*: Tallulah (McGehee); *Plaquemines Co.*: Buras (J. R. Horton); Naomi [as "Naomie"] (c.u.); *Rapides Co.*: Alexandria (E. S. Tucker); **Mississippi**: *Adams Co.*: Natchez (G. W. Alexander); *Clarke Co.*: Quitman (Murphree); *Clay Co.*: Cedar Bluff (c.u.); Cedar Bluff, Trimcane (G. W. Haug); *Harrison Co.*: Landon (Murphree); *Humphreys Co.*: Belzoni (Murphree); *Jones Co.*: Laurel (M. R. Smith); *Lowndes Co.*: Columbus (Murphree); *Monroe Co.*: Aberdeen (Murphree); *Oktibbeha Co.*: Maben (L. C. Murphree); Starkville (W. W. Love; M. R. Smith); State College [as "Agr. Col. Miss."] (M. R. Smith); *Stone Co.*: Bond (Murphree); Wiggins (Murphree); *Washington Co.*: Greenville (G. L. Snodgrass); **Missouri**: *Boone Co.*: Columbia (A. C. Cole; L. Haseman; M. Talbot); *Butler Co.*: Poplar Bluff (D. E. Read); *Cape Girardeau Co.*: Cape Girardeau (D. E. Read); *Cole Co.*: Jefferson City (A. C. Burrill); *Johnson Co.*: Knob Noster State Park (M. B. & J. R. DuBois); *Ripley Co.*: Doniphan (Pergande); *St. Charles Co.*: St. Charles (M. Talbot); *St. Louis Co.*: Webster Groves [as "Webster Grove"] (G. Loeffel); **New Mexico**: *Colfax Co.*: Cimarron Canyon, Cimarron (A. C. Cole); *Dona Ana Co.*: 45km NE Las Cruces (W. MacKay); University Ranch (C. A. Kay); *Grant Co.*: 5km NW Silver City, 1900m (P. S. Ward); I-10, 3mi E Separ (R. A. Johnson); *Hidalgo Co.*: 4km N Rodeo, 1250m (P. S. Ward); San Simon Valley, 0.25mi W jct. Rte. 80 on Portal Rd. (NM533), 4250 ft. (K. Helms); San Simon Valley, 0.3mi NE jct. State Line Rd. & Rte. 533, 4250 ft. (S. P. Cover); San Simon Valley, 0.5mi W jct. Rte. 80 on Portal Rd. (NM533), 4250 ft. (D. Gordon); San Simon Valley, jct. State Line Rd. & Portal Rd. (NM533), 4250 ft. (S. P. Cover); *Santa Fe Co.*: Santa Fe (W. M. Mann); Santa Fe, 0.5mi N I-25 on Cerillos Rd., 6200 ft. (S. P. Cover); *Sierra Co.*: Hillsboro, 1600m (P. S. Ward); *Socorro Co.*: Sevilleta NWR (M. Kaspari); *Torrance Co.*: 10mi S Mountainair, 6650 ft. (A. C. Cole); *Union Co.*: Clayton (W. M. Wheeler); **North Carolina**: *Swain Co.*: Great Smoky Mts. Natl. Park, 5500 ft. (E. S. Ross); **Oklahoma**: *Cimarron Co.*: Kenton (T. H. Hubbell); *Kay Co.*: Ponca City (A. C. Burrill); **Tennessee**: *Chester Co.*: Henderson (Murphree); *Davidson Co.*: Nashville (W. S. Creighton; A. R. Laskey); near Nashville (L. Wesson); *Hawkins Co.*: Rogersville (W. S. Creighton); *Knox Co.*: Knoxville (A. C. Cole); *McMinn Co.*: Athens (Murphree); *Monroe Co.*: no specific locality (Jones); *Shelby Co.*: Memphis (Murphree); *Wayne Co.*: Clifton (Murphree); **Texas**: *Bell Co.*: Bowmer Ranch (J. F. Watkins); *Bexar Co.*: 20mi S San Antonio (E. S. Ross); San Antonio (E. S. Ross); *Calhoun Co.*: Port Lavaca (McGehee); *Dallas Co.*: Dallas (F. C. Bishop; E. W. Laake; W. D. Pierce; Vanderford); *Grimes Co.*: Shiro (W. Buren); *Hall Co.*: 6mi SE Turkey (C. W. O'Brien); *Harris Co.*: Houston (H. C. Milleridge); *Jeff Davis Co.*: Fort Davis State Park (J. F. Watkins); *McLennan Co.*: Waco (R. S. Baldridge; J. F. Watkins); *Montgomery Co.*: Willis (J. C. Bridwell); *Travis Co.*: Austin (W. M. Wheeler); *Val Verde Co.*: Del Rio (c.u.).; **West Virginia**: *Mason Co.*: West Columbia (Murphree).

(2) Form with shiny head (CASC, CDAE, JTLC, LACM, MCZC, UCDC, USNM)

UNITED STATES **California**: *Amador Co.*: 9km WNW Plymouth, 200m (P. S. Ward); *Colusa Co.*: 1km W Fouts Springs, 600m (P. S. Ward); *Contra Costa Co.*: Danville [as "Dannville"] (F. X. Williams); *El Dorado Co.*: 14km NW Shingle Springs, 340m (P. S. Ward); 9km SW Pilot Hill, 340m (P. S. Ward); *Kern Co.*: Lonetree Cyn., 6.8mi S jct. Randsburg [as "Randsbury"] Rd. & Hwy 14 (F. Andrews & M. Wasbauer); *Lake Co.*: 14km ENE Lower Lake, 290m (P. S. Ward); 19km ESE Lower Lake, 700m (P. S. Ward); 20km ESE Lower Lake (B. L. Fisher); 6km NW Middletown, 490m (P. S. Ward); Nice-Bartlett Sprgs (A. Andrasfalvy); *Los*

Angeles Co.: Los Angeles (A. Mallis); Pearblossom Hwy & Barrel Spr. Rd. (G. C. Snelling); *Mendocino Co.*: Hopland Field Stn., 240m (P. S. Ward); *Monterey Co.*: 10km SSW Jolon, Fort Hunter Liggett MR, 340m (P. S. Ward); 14km SW Jolon, Fort Hunter Liggett MR, 640m (P. S. Ward); 15km SW Jolon, Fort Hunter Liggett MR, 490m (P. S. Ward); Paraiso Springs (c.u.); *Napa Co.*: 5km ENE Rutherford, 120m (P. S. Ward); 5km W Oakville, 560m (P. S. Ward); N. side Howell Mtn., 3km NNE Angwin, 396m (H. B. Leech); *Placer Co.*: 2km E Colfax, 490m (P. S. Ward); *Riverside Co.*: Red Cloud Mine, Chuckwalla Mts., 2700 ft. (G. C. Snelling); *San Benito Co.*: 16.8mi N New Idria (A. J. Gilbert & N. Smith); *San Bernardino Co.*: Cima (c.u.); *San Luis Obispo Co.*: 19km SSE California Valley, Carrizo Plain Natural Area, 800m (P. S. Ward); 2.5mi. S Arroyo Grande (G. I. Stage); 20km ESE California Valley, Carrizo Plain Natural Area, 800m (P. S. Ward); *Santa Barbara Co.*: Arroyo Burro, 800m (J. Longino); Cachuma Saddle, 1100m (J. Longino); Cachuma Saddle, Los Padres N. F., 930m (P. S. Ward); N end Sedgwick Ranch, 610m (P. S. Ward); N end Sedgwick Ranch, 730m (P. S. Ward); near top of Las Cruces Mts (Heath); *Solano Co.*: 2km SE Mt. Vaca, 680m (P. S. Ward); Cold Canyon, 19km NNW Vacaville, 120m (D. M. Olson; P. S. Ward); Cold Canyon, 19km NNW Vacaville, 300m (P. S. Ward); Cold Canyon, 19km NNW Vacaville, 360m (P. S. Ward); Cold Canyon, 19km NNW Vacaville, 420m (P. S. Ward); Cold Canyon, 19km NNW Vacaville, 600m (P. S. Ward); Pleasants Ridge, 530m (P. S. Ward); *Sonoma Co.*: 1km NNE Sonoma, 170m (P. S. Ward); 3km N Sonoma, 290m (P. S. Ward); 8km NNW Cazadero, 300m (P. S. Ward); Pepperwood Ranch, 15km N Santa Rosa, 360m (P. S. Ward); *Stanislaus Co.*: Del Puerto Canyon, 18km WSW Patterson, 300m (P. S. Ward); *Tulare Co.*: Ash Mtn. Kwh Pwr Stn. #3 (J. A. Halstead); *Tuolumne Co.*: 2mi SE jct. Hwy. 49 & 120, 1840 ft. (G. C. Snelling); *Yolo Co.*: 6km SW Winters, 45m (D. A. Holway); 8km SE Davis, 10m (P. S. Ward); Davis (J. J. DuBois; A. Mallis); Woodland (E. I. Schlinger); **Colorado**: *Montezuma Co.*: Mesa Verde N. P., 6300 ft. (E. V. Gregg); **Nevada**: *Lyon Co.*: East Walker River, 26km SSE Yerington, 1460m (P. S. Ward); Weeks, 1280m (P. S. Ward); **Utah**: Millard Co.: White Sage Valley [as "White Valley"] (R. W. Fautin); *Washington Co.*: Springdale, 0.25mi S Zion Natl. Park (G. C. Snelling).

Note. Workers from sites in Los Angeles County, California are intermediate in sculpture between the two forms.

Neivamyrmex texanus Watkins 1972

Neivamyrmex texanus Watkins 1972: 353. Holotype male, Austin, Texas (W. M. Wheeler) (MCZC) [examined].

Neivamyrmex nigrescens; Watkins 1972: 358 (part).

Worker measurements.—(n = 22). HW 0.71–1.42, HL 0.81–1.38, WL 1.27–2.26, MTL 0.87–1.68, CI 0.83–1.06, FCI 0.066–0.125, SI 0.70–0.93, MTI 1.18–1.48, PLI 0.78–0.96, PWI 0.58–0.74.

Worker diagnosis.—Rather large body size (see HW, HL and MTL measurements); mandible with blunt basal tooth in largest workers, such a tooth becoming indistinct to absent in smallest workers; basal margin of mandible rounding into masticatory margin; frontal carinae well separated (MFC 0.047–0.168); clypeal apron conspicuous but less well developed than in *nigrescens*; scapes relatively long, SI > 0.69 (see also plot of SL on HW; Fig. 18); occipital lobes generally well developed; anterior margin of pronotum with transverse ridge well developed; dorsal face of propodeum conspicuously depressed below the level of the promesonotum, and forming a subangulate juncture with the declivitous face, the latter more or less concave in profile; legs relatively long, MTL/HW (=MTI) > 1.15; petiole subrectangular, variable in shape (see PLI and PWI values), always longer than high or wide, although generally shorter and higher than in *nigrescens*. Head, mesosoma, petiole and postpetiole densely punctulate, and having an opaque, granular appearance. Most of the surface of metapleural gland bulla densely punctulate and opaque, although sometimes with a very small, thin shiny strip immediately above the flange of the metapleural gland orifice. Body varying from dark reddish-brown to blackish-brown, the gaster and legs lighter.

Queen diagnosis.—Eye distinct, consisting of single convex ommatidium. Head slightly broader than long (CI 1.05–1.12, n = 5). Occipital corners rounded. Pronotum with a distinct posterior dorsolateral projection (Watkins, 1972, fig. 11). Mesonotum and propodeum without a median longitudinal impression, but propodeum with a shallow longitudinal concavity. Metatibial index (MTI) 0.81–0.90 (n = 5).

Petiole transverse, markedly broader than long (PWI approximately 1.2–1.7) and, in lateral view, with a single convex anterodorsal face. Petiole width only slightly less than the length of the metatibia, DPW/MTL = 0.75–0.91 (n = 4). Length of gaster (non-physogastric) approximately twice WL (QGL/WL = 1.88–2.25, n = 3).

Male diagnosis.—Mandibles broad, spatulate (not sickle-shaped). Ocelli moderate in size and separated from the upper margin of the compound eye by a distance greater than twice the diameter of the median oecllus. No prominent transverse swelling above antennal fossa. Setae on venter of petiole long, golden, erect or suberect. Gaster reddish-brown. In profile, paramere (= stipes) slender, with a truncate posterior margin, and a tall, angular posterodorsal projection (Watkins 1985, Plate 9, fig. 5); volsella unforked, with long, slender upturned apex; aedeagus (=sagitta) with straight posteroventral process, just exceeding the posterodorsal process (in posterior reach).

Comments.—Despite the distinctive males and queens of this species, workers of *N. texanus* are difficult to distinguish from those of *N. nigrescens*. As Watkins (1972, 1985) noted, workers of *N. texanus* have the declivitous face of the propodeum slightly concave in profile (more or less straight in *N. nigrescens*), and forming a more distinctive angle with the dorsal face of the propodeum, but the difference is a subtle one. Workers of *N. texanus* also have the frontal carinae more widely separated than those of *N. nigrescens*, and plots of MFC (the minimum distance between the frontal carinae) against various measures of body size (e.g., HW, HL, MTL) reveal strong and almost diagnostic differences (Figs. 31–33), when considering those populations of *N. nigrescens* in the Southwest and eastern United States that are sympatric with *N. texanus*. Workers of *N. texanus* also tend to have a shorter, higher petiole than those of *N. nigrescens* (Fig. 34). Finally, the swelling of the metapleural gland (bulla) is densely punctulate and more or less opaque over nearly all its surface in workers of *N. texanus*, while in *N. nigrescens* it presents a more shiny appearance. Differences between *N. texanus* and *N. californicus* have been considered under the latter species.

Material examined.—(CASC, LACM, MCZC, RAJC, UCDC, USNM)

MEXICO **Chihuahua**: Mpio. Riva Palacio, Bellavista (W. & E. MacKay); Mpio Chihuahua, 45km S Sueco (Carnada); **Durango**: 37mi W Durango (W. S. Creighton); **Hidalgo**: 5mi S Tizacuya (W. S. Ross); Guerrero Mill (W. M. Mann); Pachuca (W. M. Mann); San Miguel (W. M. Mann); **Jalisco**: Guadalajara (McClendon; W. M. Mann; Cadwallader); Japopan (Cadwallader); **Nuevo León**: Vallecillo (W. F. Buren); **Sonora**: 10mi S Agua Prieta (V. Roth); 26mi NW Bahia Kino (E. M. Fisher).

UNITED STATES **Arizona**: *Cochise Co.*: 5.8mi SE Sunnyside, 5700 ft. (R. R. Snelling); 8.1mi SE Sunnyside, 5950 ft. (R. R. Snelling); Chiricahua Mts., Rucker Camp, T19S R29E Sect.22 (W. MacKay); Douglas (W. W. Jones); Huachuca Mtns., 3mi SW Rte. 92 on Coronado Natl. Mon. Rd., 5100 ft. (S. P. Cover); Huachuca Mtns., 3mi S jct. Rt. 92 on rd. to Coronado Natl. Mon., 5100 ft. (S. P. Cover); Huachuca Mtns., Bear Creek, 19km SW Sierra Vista, 1640m (S. G. Brady); Palmerlee, Huachuca Mtns., 5300 ft. (W. M. Wheeler); San Bernardino Valley, 1mi NW jct. Rt. 80 on FSR 74 (Rucker Canyon Road), 4700 ft. (S. P. Cover); *Pima Co.*: 16mi W Tucson (S. Prchal; G. C. Snelling); Baboquivari Mtns, Brown Canyon (A. C. Cole); Baboquivari Mtns, Forestry Cabin, 3500 ft. (W. S. Creighton); Brown Canyon, Baboquivari Mtns. (Menke & Stange); Sabino Canyon (R. H. Crandall); Tucson Mtns. (F. R. Gehlbach); *Santa Cruz Co.*: Nogales (Buren); **Colorado**: *El Paso Co.*: Colorado Springs (J. G. Jack); Colorado Springs and vicinity (W. M. Wheeler); *Jefferson Co.*: Prospect Park (c.u.); **Florida**: *Alachua Co.*: 29°34.5'N, 82°29'W (R. W. Lundgren); Austin Carey Forest, Gainesville (G. B. Fairchild); Gainesville (T. H. Hubbell; A. Van Pelt); Pierce Homestead, Gainesville (W. R. Pierce); *Escambia Co.*: Pensacola (R. M. Lhamon); *Indian River Co.*: Sebastian (Nelson); *Leon Co.*: Woodville (D. E. Read); *Volusia Co.*: Daytona [Beach] (W. F. Buren); **New Mexico**: *Dona Ana Co.*: 45km NE Las Cruces (W. MacKay); *Eddy Co.*: Los Medanos, T22S R31E, Sect.15 (c.u.); *San Miguel Co.*: Las Vegas (W. M. Wheeler); **North Carolina**: *New Hanover Co.*: Wilmington (Vanderford); *Yancey Co.*(?): Black Mts. (c.u.); **South Carolina**: *Oconee Co.*: Clemson College (J. Berly & M. Smith); **Texas**: *Bexar Co.*: San Antonio (E. S. Ross); *Crockett Co.*: Ozona (A. C. Cole); *Jeff Davis Co.*: Fort Davis (T. W. Taylor); *Kimble Co.*: Junction (J. F. Watkins); *Llano Co.*: Llano (A. W. Morrill); *McLennan Co.*: Baylor Camp (J. F. Watkins); Waco (J.

Briga; S. Davis; S. Eldridge; F. R. Gehlbach; O. L. Nicholson; R. W. Plsek; C. A. Rhines; J. F. Watkins); *Taylor Co.*: Abilene rest stop (W. S. Creighton); *Travis Co.*: Austin (W. M. Wheeler); Austin, Brackenridge Field Lab (S. D. Porter); *Victoria Co.*: Victoria (c.u.).; **Virginia**: *Chesterfield Co.*: Warwick (Bond); *Essex Co.*: 1mi SE Dunnsville (D. R. Smith); *Henry Co.*: Chatmoss Plant, Martinsville (S. Schaeffer); *Louisa Co.*: 4mi S Cuckoo (J. Kloke & D. R. Smith); *Norfolk city*: Norfolk (Vanderford).

MODIFICATION OF EXISTING IDENTIFICATION KEYS

Couplets 5 and 9 of Watkins' (1985) worker key to the United States species of *Neivamyrmex* need modification to take into account the much greater intraspecific variability in body sculpture in *N. nigrescens*. In the updated portions of the key (below) I have also documented additional features of *N. texanus* and *N. opacithorax* which will facilitate their identification.

5 In lateral view declivitous face of propodeum slightly concave and forming a somewhat angular corner with the dorsal (basal) surface; frontal carinae well separated (MFC 0.05–0.17), as revealed in bivariate plots of MFC on various measures of body size (Figs. 31–33); petiole relatively short and high (Fig. 34); surface of most of the metapleural gland bulla densely punctulate and opaque, although sometimes with a very small, thin shiny strip immediately above the flange of the metapleural gland orifice . . . ***N. texanus* Watkins**

– Declivitous face of propodeum more or less straight in lateral view and forming a rounded angle with the dorsal (basal) surface; frontal carinae usually more closely contiguous (Figs. 31–33) and petiole height tending to be lower (Fig. 34); sculpture on surface of metapleural gland bulla becoming obsolete, such that the lower half or more is smooth (or weakly reticulate) and conspicuously shiny . . . . . ***N. nigrescens* (Cresson) (part)**

9 Inner basal margin of mandible with a straight edge which forms an angular corner or small tooth at its juncture with the masticatory margin; side of pronotum usually smooth and shiny, and contrasting with the rugulose-punctulate sculpture that covers at least part of the mesosoma dorsum . . . . . ***N. opacithorax* (Emery)**

– Inner basal margin of mandible with a convex edge which curves into the masticatory margin without forming an angular corner (Fig. 1); pronotal sculpture variable, but side of pronotum usually at least weakly reticulate-punctulate rather than exhibiting a smooth, shiny surface that contrasts with the sculptured mesosoma dorsum 9A

9A Body, scapes and legs shorter, head broader; MTI 1.05–1.14; see also plots of MTL on HW, SL on HW, WL on HW, CI on MTL and SI on MTL (Figs. 17–19, 21–23, 25, 26); dorsal surface of propodeum only slightly depressed below the level of the mesonotum (Fig. 2); dorsum of postpetiole and (typically) center of mesonotum smooth and shining, with scattered piligerous punctures but little or no trace of reticulation or punctulae . . . . . ***N. californicus* (Mayr)**

– Body, scapes and legs longer; MTI 1.16–1.52; see also Figs. 17–19, 21–23, 25, 26; dorsal surface of propodeum conspicuously depressed below the level of the mesonotum (Fig. 5); postpetiole and mesonotum varying from opaque to sublucid, with traces of reticulation or punctulae usually evident . . . . . ***N. nigrescens* (Cresson) (part)**

In the key to United States *Neivamyrmex* based on queens (Watkins 1972: 350–351) "*californicus*" in couplet 7 should be replaced with "*nigrescens* (part)". The queen of *N. californicus* is not yet definitively known (see discussion above, under that species).

Couplet 8 of Watkins' (1982) key to Mexican species of *Neivamyrmex* can be modified as follows to incorporate *N. californicus* and the more recently described *N. chamelensis* Watkins (1986). The treatment of *N. nigrescens* requires no change since the shiny form of *N. nigrescens* is not known to occur in Mexico.

8 Head and gaster of smaller workers blackish brown or reddish brown with a black overcast, mesosoma reddish brown without a blackish overcast; dorsum of promesonotum

slightly convex, and dorsum of propodeum as short or shorter than the node of petiole in lateral view ..... *N. manni* **(Wheeler)**

– Head and mesosoma same color (reddish brown), gaster slightly lighter; posterior one-half of promesonotum flattened; dorsum of propodeum variable in length 8A

8A Dorsal face of propodeum shorter than the declivitous face, and conspicuously depressed below the level of the promesonotum, at least in larger workers (Watkins 1986, fig. 2); postpetiole as long as petiole ..... *N. chamelensis* **Watkins**

– Dorsal face of propodeum as long as, or longer than, the declivitous face, and not conspicuously depressed below the level of the promesonotum (Fig. 2); postpetiole shorter than petiole 8B

8B Inner basal margin of mandible with a straight edge which forms an angular corner or small tooth at its juncture with the masticatory margin; clypeal apron short, extending anteriorly by a distance equal to about 0.2–0.4 times the diameter of the torulus; petiole relatively narrow (Fig. 20); side of pronotum usually smooth and shiny, and contrasting with the rugulose-punctulate sculpture that covers at least part of the mesosoma dorsum ..... *N. opacithorax* **(Emery)**

– Inner basal margin of mandible with a convex edge which curves into the masticatory margin without forming an angular corner (Fig. 1); clypeal apron longer, extending anteriorly by a distance equal to about 0.4–0.5 times the diameter of the torulus; petiole broader (Fig. 20); pronotal sculpture variable, but side of pronotum usually at least weakly reticulate-punctulate rather than exhibiting a smooth, shiny surface that contrasts with the sculptured mesosoma dorsum ..... *N. californicus* **(Mayr)**

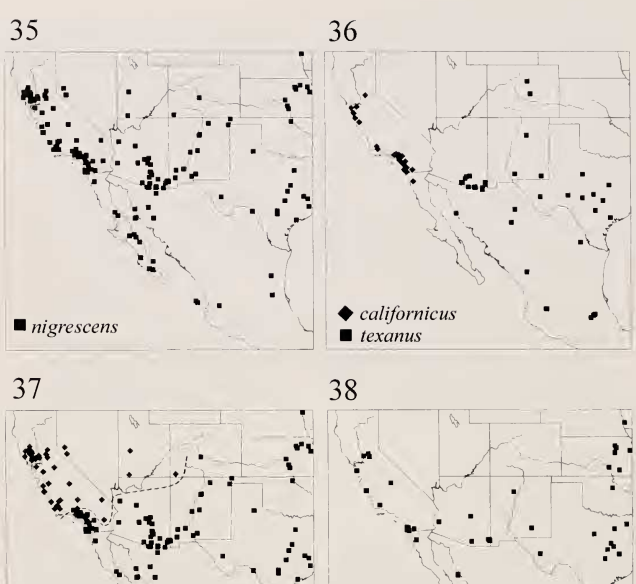
BIOLOGICAL OBSERVATIONS

Habitat Preferences

Although *N. nigrescens* and *N. californicus* are probably not sister taxa (see below) they appear to have similar ecological preferences in California. In southern California and northern Baja California, where morphological differences between the two species are greatest, their geographical distributions overlap broadly (Figs. 35, 36) and they occur together in such habitats as chaparral, coastal sage scrub and oak woodland. In northern California workers of *N. nigrescens* are more difficult to distinguish from those of *N. californicus*, due to convergence in body sculpture. In this region the two species are less frequently sympatric. *N. californicus* tends to be confined to more mesic, coastal locations than *N. nigrescens*, although the habitats occupied are similar: oak woodland, riparian woodland, chaparral and grassland. An exception to this is the occurrence of *N. californicus* at a xeric inland site in the Sierra Nevada foothills (14km NW Shingle Springs, El Dorado County) where it co-occurs with *N. nigrescens* and *N. opacithorax* in a distinctive chaparral vegetation on gabbro soil. It was the sympatric association at this locality that alerted me to the distinction between true *N. californicus* and the "shiny morph" of *N. nigrescens*. The gabbro site has a number of rare plant species (Hunter and Horenstein 1992) and *N. californicus* likewise gives the impression of being an isolated, relic population here (the northern-most point in Fig. 36).

Throughout California both *N. californicus* and *N. nigrescens* are limited to low elevations, essentially below the coniferous forest zones. Most recorded populations come from locations below 1500m (*N. californicus*: sea level to 1840m; *N. nigrescens*: sea level to 1460m).

Outside the range of *N. californicus*, populations of *N. nigrescens* show a wide latitude of habitat choice, being found in scrubland, grassland and canyons of the



Figs. 35–38. Known distributions in southwestern United States and Mexico of *Neivamyrmex nigrescens* (25), *N. californicus* and *N. texanus* (26), shiny and punctate forms of *N. nigrescens* (27), and *N. opacithorax* (28). *N. nigrescens*, *N. opacithorax* and *N. texanus* also occur in eastern United States (see Watkins 1985: 499–500).

Sonoran and Chihuahuan deserts, pine-oak-juniper woodland, prairie grassland, and eastern deciduous forest (Gregg 1963; Mirenda *et al.* 1980; Schneirla 1958; Smith 1942). It is perhaps unsurprising that over this broad range of ecological conditions the species displays considerable intraspecific variation in worker morphology.

Associations with *Messor andrei*

In California both *Neivamyrmex nigrescens* and *N. californicus* are often associated with nests of the common seed-harvesting ant, *Messor andrei* (Mayr). Indeed, one of the most efficient ways to determine the presence of these species at a locality is to examine the chaff piles of *Messor andrei*

nests. Such middens frequently contain the corpses of *Neivamyrmex* workers. There are several possible explanations for this.

First, *Messor andrei* workers appear to be efficient scavengers that collect dead and dying ants (of all kinds) and later discard the dried corpses in their middens. This is indicated by the fact that the remains of other ants, including species of *Camponotus, Crematogaster, Dorymyrmex, Forelius, Formica, Leptothorax, Monomorium, Pheidole, Prenolepis, Solenopsis* and *Stenamma*, are often encountered in *M. andrei* middens (Ward, pers. obs.).

Second, both *N. californicus* and *N. nigrescens* have been observed attacking nests of *Messor andrei*. In Amador County, California I observed nocturnal foraging columns of *N. nigrescens* workers entering two adjacent *M. andrei* nests—one containing a large *Messor* colony, the other a small incipient colony. The raid on the small nest was partially successfully, with *N. nigrescens* workers carrying off paralyzed *Messor* worker minims, although some *Messor* workers (and a dealate queen) escaped capture by climbing short grass stalks. No prey were observed to be taken from the larger nest, which contained normal-sized *Messor* workers. Mark Brown (1999) recorded *N. californicus* workers attacking *Messor andrei* nests at Jasper Ridge Preserve, near Stanford University. These raids on *Messor andrei* nests by *N. californicus* and *N. nigrescens* do not appear to be especially effective, yet in the observed cases the army ants persisted in their assaults.

Third, the high frequency of *Neivamyrmex* worker corpses in *Messor* middens may reflect a tendency of *Neivamyrmex* colonies to temporarily occupy part of the underground chambers of the *Messor* nests, leading to an increased frequency of interactions between the two species. Some evidence for this comes from an observation that I made in early April 1984 near Rutherford, Napa County, northern California: a colony of *N. nigrescens* ("shiny form"), containing larvae, was located in wet but well-aerated soil immediately adjacent to an active *Messor andrei* nest. The *N. nigrescens* workers were emerging from the soil and slowly milling about on the ground surface during daylight hours, an unusual behavior but one which occurs in spring (March–May) in northern California before *N. nigrescens* begins its period of summer-active—and predominantly nocturnal—surface raiding. Thus, it appeared that this Rutherford colony of *N. nigrescens* had over-wintered in the soil in abandoned sections of the *Messor andrei* nest. Schneirla (1963) reported the use of pre-empted ant nests (species not specified) by over-wintering colonies of *N. nigrescens* in Arizona.

Interactions with Other California Ant Species

Other ants besides *Messor andrei* that are subject to raids by *Neivamyrmex nigrescens* in California include *Pheidole californica* Mayr, *P. hyatti, Solenopsis molesta* (Say) and *Formica moki* Wheeler (Ward, pers. obs.). Mallis (1938, 1941) reported *N. nigrescens* (misidentified as *N. californicus*) foraging nocturnally for insects attracted to street lamps on the Davis campus of the University of California, and attacking nests of the introduced ant, *Tetramorium caespitum* (Linnaeus). At the same location Mallis (1938) also recorded an altercation between *Neivamyrmex* and Argentine ants, *Linepithema humile* (Mayr), in which *Linepithema* emerged the victor. *L. humile* is now very abundant on the UC Davis campus and, during 17 years of observation here, I have seen no evidence that populations of *Neivamyrmex nigrescens* survive on campus, although the species occurs 8km southeast of Davis at a site not yet overrun by *Linepithema humile*. Work by Suarez *et al.* (1998) in southern California shows that *Neivamyrmex* species, including *N. nigrescens*, are among the first ant species to disappear from patches of remnant coastal sage scrub when *Linepithema humile* invades from adjacent urban habitat.

Table 1. Tests of nest evacuation response in potential prey of *Neivamyrmex*. Each test involved placement of one to several live *Neivamyrmex* workers at the nest entrance of an active test ant colony. All locations are in California.

Test species	Location	*Neivamyrmex* species (and source population)	Mass evacuation response?
Pheidole desertorum	Pinyon Flats	*nigrescens* (Pinyon Flats)	Yes
Pheidole hyatti	Carrizo Plain	*nigrescens* (Carrizo Plain)	Yes
Pheidole hyatti	Del Puerto Canyon	*nigrescens* (Cold Canyon)	Yes
Pheidole californica	Cold Canyon	*californicus* (El Dorado Co.)	Yes
Pheidole californica	Cold Canyon	*nigrescens* (Cold Canyon)	Yes
Pheidole californica	Davis	*nigrescens* (Cold Canyon)	Variable[a]
Pheidole californica	Davis	*nigrescens* (Carrizo Plain)	No
Pheidole californica	Del Puerto Canyon	*nigrescens* (Cold Canyon)	No
Pheidole californica	Ventura Co.	*nigrescens* (Carrizo Plain)	No
Pheidole californica	El Dorado Co.	*opacithorax* (El Dorado Co.)	No
Messor andrei	Cold Canyon	*nigrescens* (Cold Canyon)	No
Dorymyrmex bicolor	Pinyon Flats	*nigrescens* (Pinyon Flats)	No
Dorymyrmex insanus	Davis	*nigrescens* (Cold Canyon)	No

[a] Evacuation response seen in one of two trials.

Elsewhere, across its broad transcontinental distribution, *N. nigrescens* is reported to preferentially raid ant nests, especially those of *Pheidole* species (Mirenda *et al.* 1980), but also including colonies of *Aphaenogaster*, *Camponotus*, *Dorymyrmex*, *Formica*, *Leptothorax* and *Solenopsis* (LaMon and Topoff 1981; Mirenda *et al.* 1980; Schneirla 1958, 1963; Smith, 1927). Both ant brood, adult workers, and (when available) sexual alates are taken as prey, as are occasionally termites and non-social insects.

Less is known about the prey preferences of *Neivamyrmex californicus* but they appear to be similar to those of *N. nigrescens*. Mark Brown (1999) observed *N. californicus* attacking both *Messor andrei* and *Pheidole californica* colonies at Jasper Ridge. There is indirect evidence that *Solenopsis molesta* and *Pheidole hyatti* are also preyed upon. In a collection of dead *N. californicus* workers from a *Messor andrei* chaff pile at Jasper Ridge (collected by Nate Sanders) several individuals had dead workers of *Solenopsis molesta* attached (with closed mandibles) to legs and/or antennae. Dead workers of *N. californicus* (as well as those of *N. nigrescens*) have been found in the nest middens of *Pheidole hyatti* (Ward, pers. obs.). This and certain other *Pheidole* species in California show an enemy-specific nest evacuation response to the presence of *N. californicus* and *N. nigrescens* workers.

Observations on this nest absconding behavior in California *Pheidole* are summarized in Table 1. A single *Neivamyrmex* worker, held with a pair of forceps at the nest entrance, can be sufficient to cause mass evacuation of workers and brood in *Pheidole californica*, *P. desertorum*, and *P. hyatti*. In *Pheidole californica* the response is not invariably observed, however (Table 1), and seems to vary with location, ambient conditions, and possibly as a function of previous experience (as documented for another prey species, *Aphaenogaster cockerelli* André (McDonald and Topoff 1986)). Similar nest evacuation behavior has been studied in Arizona populations of *Pheidole desertorum* and *P. hyatti* attacked by *N. nigrescens* (Droual 1983, 1984).

POPULATION DIFFERENTIATION AND BIOGEOGRAPHY

The taxonomic confusion surrounding *N. californicus* and *N. nigrescens* can be traced to undue reliance on superficial features of head sculpture, lack of attention

to other structural differences, and insufficient appreciation of the degree of variability in *N. nigrescens*. In *Neivamyrmex* and in all other genera of New World army ants (which together comprise the subfamily Ecitoninae) the queens are entirely wingless and have limited capacities for dispersal (Gotwald 1995). Because of the population viscosity associated with limited female movement—only partly mitigated by gene flow via dispersing, winged males—and perhaps also because of the lower effective population sizes achieved by these highly predacious (and hence higher trophic level) organisms, one *expects* conspecific allopatric populations of army ants to develop substantial differences. The prediction is borne out, at least among the more widespread species of ecitonine army ants, in which there exists a large amount of geographical variation (Borgmeier 1955, 1956). It seems desirable for taxonomists to be cautious in establishing new species of army ants especially when dealing with closely related allopatric populations. In the present paper I have refrained from giving a new name to the shiny form of *N. nigrescens*, because it is essentially allopatric to the more typical granulate-punctate *N. nigrescens*. The two are not known to both occur sympatricly *and* retain their distinctness; rather, in geographically intermediate localities (i.e., in the San Gabriel Mountains of southern California) we find morphologically transitional populations. A genetic analysis of the transition zone would be interesting, especially in view of its relative narrowness.

Thus, the distribution of the two forms of *N. nigrescens* (Figure 37) suggests a previous fragmentation of the range of *N. nigrescens*, and the consequent differentiation of populations but not to a degree sufficient to cause reproductive isolation. The Transverse Ranges of California and the upper Colorado River basin emerge as the probable sites of geographic barriers.

The divergence between the common ancestor of *N. nigrescens* (sensu lato) and *N. californicus* must have occurred considerably earlier. On the basis of structural similarities (Figs. 17–19) *N. californicus* actually appears to be more closely related to *N. opacithorax* than to *N. nigrescens*, with the latter species being more closely related to *N. texanus*. This hypothesis could be tested with the study of additional characters and (crucially) the inclusion of additional taxa from Mexico, especially *N. chamelensis*, *N. cornutus*, *N. manni*, and *N. sumichrasti*. The possibility that the widespread *N. nigrescens* is paraphyletic should also be considered.

A final point of biogeographic interest concerns the distribution limits of *Neivamyrmex californicus* (Fig. 36) and *N. opacithorax* (Fig. 38) in northern California. Both species appear to be restricted to areas east and south of the Sacramento River and the San Francisco/San Pablo Bays. This drainage system can be expected to be a significant barrier to dispersal in hymenopterans such as army ants whose reproductive females are wingless.

ACKNOWLEDGMENTS

I am grateful to the following persons for access to material in collections: Wojciech Pulawski (CASC), John Sorensen (CDAE), Jack Longino (JTLC), Roy Snelling (LACM), Stefan Cover (MCZC), Ivan Löbl (MHNG), Stefan Schödl (NHMV), and Ted Schultz (USNM). Additional useful material was received from Melissa Bennett, Seán Brady, Don Feener, Robert Johnson, Mike Kaspari, Nate Sanders, Gordon Snelling, Andy Suarez and Mark Trepanier. I thank Seán Brady, Brian Fisher, Jack Longino and two anonymous reviewers for comments on the manuscript. Research support was received from the University of California and the National Science Foundation.

LITERATURE CITED

Bolton, B. 1995. *A new general catalogue of the ants of the world*. Cambridge, Massachusetts: Harvard University Press, 504 pp.

Borgmeier, T. 1953. Vorarbeiten zu einer Revision der neotropischen Wanderameisen. *Studia Entomologica* 2: 1–51.

Borgmeier, T. 1955. Die Wanderameisen der neotropischen Region. *Studia Entomologica* 3: 1–720.

Borgmeier, T. 1956. Ueber Rassen bei *Eciton* (Hym. Formicidae). *Revista Brasileira de Entomologia* 4: 209–212.

Borgmeier, T. 1958. Nachtraege zu meiner Monographie der neotropischen Wanderameisen (Hym. Formicidae). *Studia Entomologica* (n.s.)1: 197–208.

Brown, M. J. F. 1999. Nest relocation and encounters between colonies of the seed-harvesting ant *Messor andrei*. *Insectes Sociaux*, in press.

Creighton, W. S. 1950. The ants of North America. *Bulletin of the Museum of Comparative Zoology* 104: 1–585.

Cresson, E. T. 1872. Hymenoptera Texana. *Transactions of the American Entomological Society* 4: 153–292.

Dalla Torre, K. W. v. 1893. *Catalogus Hymenopterorum hucusque descriptorum systematicus et synonymicus*. Vol. 7. Formicidae Heterogyna. Leipzig: W. Engelmann, 289 pp.

Droual, R. 1983. The organization of nest evacuation in *Pheidole desertorum* Wheeler and *P. hyatti* Emery (Hymenoptera: Formicidae). *Behavioral Ecology and Sociobiology* 12: 203–208.

Droual, R. 1984. Anti-predator behaviour in the ant *Pheidole desertorum*: the importance of multiple nests. *Animal Behaviour* 32: 1054–1058.

Emery, C. 1894. Studi sulle formiche della fauna neotropica. VI–XVI. *Bullettino della Società Entomologica Italiana* 26: 137–241.

Emery, C. 1895. Beiträge zur Kenntniss der nordamerikanischen Ameisenfauna. Schluss. *Zoologisches Jahrbücher. Abteilung für Systematik, Geographie und Biologie der Tiere* 8: 257–360.

Emery, C. 1900. Nuovi studi sul genere *Eciton*. *Memorie della Reale Accademia delle Scienze dell'Istituto di Bologna* 58: 173–188 [pagination of separate: 511–526].

Forel, A. 1914. Formicides d'Afrique et d'Amérique nouveaux ou peu connus. *Bulletin de la Société Vaudoise des Sciences Naturelles* 50: 211–288.

Gotwald, W. H., Jr. 1995. *Army ants: the biology of social predation*. Ithaca, New York: Cornell University Press, xviii + 302 pp.

Gregg, R. E. 1963. *The ants of Colorado, with reference to their ecology, taxonomy, and geographic distribution*. Boulder: University of Colorado Press, xvi + 792 pp.

Hunter, J. C., Horenstein, J. E. 1992. The vegetation of the Pine Hill area (California) and its relation to substratum. Pp. 197–206 in: Baker, A. J. M., Proctor, J., Reeves, R. D. (eds.) The vegetation of ultramafic (serpentine) soils. Andover, U. K.: Intercept Ltd., xx + 509 pp.

LaMon, B., Topoff, H. 1981. Avoiding predation by army ants: defensive behaviours of three ant species of the genus *Camponotus*. *Animal Behaviour* 29: 1070–1081.

Mallis, A. 1938. Army ants in California. *Scientific Monthly* 47: 220–226.

Mallis, A. 1941. A list of the ants of California with notes on their habits and distribution. *Bulletin of the Southern California Academy of Sciences* 40: 61–100.

Mayr, G. 1870. Formicidae novogranadenses. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften in Wien. Mathematisch-Naturwissenschaftliche Classe. Abteilung I* 61: 370–417.

Mcdonald, P., Topoff, H. 1986. The development of defensive behavior against predation by army ants. *Developmental Psychobiology* 19: 351–368.

Mirenda, J. T., Eakins, D. G., Gravelle, K., Topoff, H. 1980. Predatory behavior and prey selection by army ants in a desert-grassland habitat. *Behavioral Ecology and Sociobiology* 7: 119–127.

Schneirla, T. C. 1958. The behavior and biology of certain Nearctic army ants. Last part of the functional season, southeastern Arizona. *Insectes Sociaux* 5: 215–255.

Schneirla, T. C. 1963. The behaviour and biology of certain Nearctic army ants: springtime resurgence of cyclic function—southeastern Arizona. *Animal Behaviour* 11: 583–595.

Smith, M. R. 1927. A contribution to the biology and distribution of one of the legionary ants, *Eciton schmitti* Emery. *Annals of the Entomological Society of America* 20: 401–404.

Smith, M. R. 1938. Notes on the legionary ants *Eciton*, subgenus *Acamatus* with a record of new specific synonymy. *Proceedings of the Entomological Society of Washington* 40: 157–160.

Smith, M. R. 1942. The legionary ants of the United States belonging to *Eciton* subgenus *Neivamyrmex* Borgmeier. *American Midland Naturalist* 27: 537–590.

Snelling, R. R., George, C. D. 1979. *The taxonomy, distribution and ecology of California desert ants*. Report to California Desert Plan Program, Bureau of Land Management, U.S. Dept. Interior. 335 + 89 pp.

Suarez, A. V., Bolger, D. T., Case, T. J. 1998. Effects of fragmentation and invasion on native ant communities in coastal southern California. *Ecology* 79: 2041–2056.

Watkins, J. F., II. 1972. The taxonomy of *Neivamyrmex texanus*, n. sp., *N. nigrescens* and *N. californicus* (Formicidae: Dorylinae), with distribution map and keys to the species of *Neivamyrmex* of the United States. *Journal of the Kansas Entomological Society* 45: 347–372.

Watkins, J. F., II. 1976. *The identification and distribution of New World army ants (Dorylinae: Formicidae)*. Waco, Texas: Baylor University Press, 102 pp.

Watkins, J. F., II. 1982. The army ants of Mexico (Hy-

menoptera: Formicidae: Ecitoninae). *Journal of the Kansas Entomological Society* 55: 197–247.

Watkins, J. F., II. 1985. The identification and distribution of the army ants of the United States of America (Hymenoptera, Formicidae, Ecitoninae). *Journal of the Kansas Entomological Society* 58: 479–502.

Watkins, J. F., II. 1986. *Neivamyrmex chamelensis*, n. sp. (Hymenoptera: Formicidae: Ecitoninae) from Jalisco, Mexico. *Journal of the Kansas Entomological Society* 59: 361–366.

Wheeler, W. M. 1900. The female of *Eciton sumichrasti* Norton, with some notes on the habits of Texan Ecitons. *American Naturalist* 34: 563–574.

Wheeler, W. M. 1908. The ants of Texas, New Mexico and Arizona. Part I. *Bulletin of the American Museum of Natural History* 24: 399–485.